Zootaxa 5497 (4): 505–519
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5497.4.3
http://zoobank.org/urn:lsid:zoobank.org:pub:0A1B7603-FB2D-46FB-9D91-643EEB0A3632

Toward a revision of the bamboo corals: Part 6, Illuminating a new candelabrum genus (Octocorallia: Keratoisididae)

SCOTT C. FRANCE[1*] & LES WATLING[2]
[1]*Department of Biology, University of Louisiana at Lafayette, Lafayette, LA 70504 USA*
france@louisiana.edu; https://orcid.org/0000-0002-2114-5968
[2]*School of Life Sciences, University of Hawaii at Manoa, Honolulu, HI 96822 USA*
watling@hawaii.edu; https://orcid.org/0000-0002-6901-1168
**Corresponding author*

ABSTRACT

Observations and collections made using remotely operated vehicles (ROV) outfit with high-definition video cameras on bathyal seamounts of the North Atlantic and North Pacific have revealed a bamboo coral (Octocorallia, Keratoisididae) with consistent and recognizable colony morphology: a long unbranched "stem" from which many vertically aligned branches arise in a single plane to produce the aspect of a tall candelabrum. Additional observations encountered colonies with only 3 branches arising from the central terminal node to produce the appearance of a standing trident. Genetic analyses suggested both colony morphologies (trident and candelabrum) to be the same species at different growth stages. Herein we formally describe this taxon, *Tridentisis candelabrum* n. gen. n. sp., erecting a new genus to accommodate the unique and distinctive colony morphology, and discuss morphological variation observed across the documented geographic range.

Key words: Deep sea, bathyal, ROV observations, taxonomy, seamounts, North Atlantic Ocean, North Pacific Ocean, morphological variation

INTRODUCTION

Our knowledge of the deep-sea coral fauna continues to expand as tools to explore and sample the deep sea are developed. On an expedition in 2005 to study the deep-sea coral communities of North Atlantic seamounts using a remotely operated vehicle (ROV) outfit with high-definition video cameras, we spotted a bamboo coral (Octocorallia, Keratoisididae) whose colony morphology was immediately recognizable as novel and distinct. The colony took on the aspect of a tall candelabrum (≈70 cm height), with a stem of ≈40 cm height topped by 11 vertically aligned branches (Figure 3A). We subsequently saw a second larger colony (with 34 vertical branches) on the same ROV dive (Figure 3D). On subsequent expeditions off Molokai, Hawaii in 2006, and the Bahamas in 2009, we encountered and sampled smaller colonies with equally distinct, consistent and recognizable colony morphology: a long unbranched "stem" from which 3 branches arise and grow vertically to produce the appearance of a standing trident. Sequencing of the *mtMutS* gene, a *de facto* molecular barcode for octocorals (McFadden *et al.* 2011), revealed both colony forms shared the same haplotype (Watling *et al.* 2022, Supplemental Table S1). Phylogenetic analyses showed this sequence haplotype (referred to as "kerI4" in van der Ham *et al.* 2009) to be unique among Keratoisididae (Watling *et al.* 2022; van der Ham *et al.* 2009). Based on the assumption that a unique *mtMutS* haplotype represents a species (Pante *et al.* 2015)—due to the slow substitution rate of the keratoisidid mt genome—we hypothesized the trident-shaped colonies to be the same species as the candelabrum form, suggesting a growth pattern wherein an initially unbranched whip-like colony gives rise to a trifurcation at a terminal node leading to 3 vertical branches, with additional bifurcations arising in a single plane from each subsequent node of the lateral-most branches. The lateral branches curve upward into vertical branches to give the colony the appearance of a balanced (around the centermost vertical branch) planar candelabrum with undulating arms. Many additional

Accepted by R. Cordeiro: 17 Jul. 2024; published: 27 Aug. 2024

in situ observations of this morphospecies at bathyal depths have come from ROV operations of the NOAA Ship *Okeanos Explorer* and Schmidt Ocean Institute's R/V *Falkor*.

Herein we formally describe this taxon, erecting a new genus to accommodate the unique and distinctive colony morphology. This paper is the sixth in a series of papers revising the bamboo corals. Reference to the earlier papers in the series can be found in part 5 (Lapointe and Watling, 2022).

Abbreviations

BPBM: Bernice P. Bishop Museum, Honolulu
SRA: NCBI Sequence Read Archive
YPM: Yale Peabody Museum, New Haven

MATERIALS AND METHODS

Specimen Collection

Specimens available for description were collected on two expeditions in the North Atlantic and two in the North Pacific. The Atlantic cruises were Deep Atlantic Stepping Stones, in 2005, and Deep-water Connections: Probing the Southern Limits of Distribution of North Atlantic Deep-Sea Coral Communities, in 2009; metadata and imagery from these expeditions are available via the online Digital Atlas (NOAA Ocean Exploration 2023). Specimens were sampled using the ROV *Hercules* in 2005 and the ROV *Global Explorer* in 2009. The Pacific cruises were conducted in 2006 and 2007 aboard the University of Hawaii's R/V *Kaimikai-o-Kanaloa* with sampling from the DSV *Pisces V*. Prior to collection, colonies were imaged *in situ* with a high-definition video or still camera. Samples were collected using a manipulator equipped with a cutting claw and subsequently stowed in an insulated collection box on the vehicle for return to the research vessel. Once on deck, specimens were kept in cold seawater until they could be fixed and preserved. Prior to preservation, specimens were photographed and labeled, small pieces of tissue were sampled for genetic analysis, and the remainder were fixed in 4% formalin for 12 h, then rinsed and stored in bags in 70% ethanol. Additional *in situ* observations came from ROV operations of the NOAA Ship *Okeanos Explorer* during the NOAA CAPSTONE expeditions from 2015–2017 and ASPIRE expeditions from 2018-2022; Schmidt Ocean Institute's R/V *Falkor* expeditions to the Emperor Seamounts and the deep waters off the Great Barrier Reef. An additional *in situ* image of an as yet unexamined specimen was received from R/V *James Cook* cruise JC094 Dive 225 on Annan (Carter) Seamount.

Morphological Analysis

For detailed morphological analysis of taxonomically informative characters, a few polyps were removed from the colony. Polyps were examined intact using both light and scanning electron microscopy (SEM). For light microscopy, the polyp tissue was cleared by soaking in absolute ethanol and clove oil. The polyp was then photographed using partially crossed polarizing filters, which helped to make the smaller sclerites visible. For SEM the polyp was soaked in absolute alcohol then dried in a Samdri Critical Point Dryer, mounted on a stub and coated with Au and Pd for 1 minute in a sputter coater. Other polyps were dissected with the tissue from the tentacles, pharynx, and body wall put into separate dishes to which standard household bleach was added. After the tissue was dissolved, the sclerites were rinsed with five changes of de-ionized water, dried, and then mounted on a stub coated with double stick tape using a 5x0 paint brush. The sclerites were then coated with Au and Pd for 1 minute.

Genetics

Genetic diversity and uniqueness of the taxon were evaluated by sequencing regions of mitochondrial DNA. Sequencing of the holotype and paratype specimens from Balanus Seamount was conducted as part of earlier studies and reported in publications by Brugler & France (2008), van der Ham *et al.* (2009) and Pante *et al.* (2012). All other

specimens available to us were sequenced at the *mtMutS* gene and included in the phylogenetic analyses reported by Watling *et al.* (2022, Supplemental Table S1). Seven specimens were additionally sequenced at the intergenic region *igr4*, following the same protocols described by van der Ham *et al.* (2009). As all the specimens yielded the same *mtMutS* haplotype, only a single representative was included in the phylogeny of Watling *et al.* (2022). For completeness, and to associate a sequence with each museum voucher specimen, we have submitted all the sequence data to GenBank and report the accession numbers in Table 1. However, as there is no new information to add due to the lack of genetic variation among the samples, we have not repeated the phylogenetic analysis.

TAXONOMY

Family Keratoisididae Gray, 1870

Tridentisis France and Watling, gen. nov.

urn:lsid:zoobank.org:act:603B6FDD-6406-401B-B351-900D80AAE74E

Type species. *Tridentisis candelabrum*, sp. nov.

Diagnosis. Colonies with a long unbranched "stem" that reaches a node from which 3 branches arise and grow vertically to produce the appearance of a trident. From this initial trifurcation, additional bifurcations arise in a single plane from each subsequent node of the lateralmost branches; the lateral growth curves upward into vertical branches to give the colony the appearance of a planar candelabrum. Branches arise from the nodes. Polyps arise on all sides of the axis. Polyps present on the main stem below the trifurcation but do not extend to the holdfast, leaving the lower stem with smooth coenenchyme. Prominent inter-tentacular needles protrude beyond the folded tentacles.

Etymology. An allusion to Neptune's trident for the early colony growth stage, and-isis, the stem group name.

Tridentisis candelabrum France and Watling, sp. nov.

urn:lsid:zoobank.org:act:D0BC20BC-6377-4A2E-B3F4-906FA285FF3C
(Figures 1 to 7)

Keratoisidinae BAL208-1: Brugler and France 2008
Keratoisidinae Undescribed A BAL208-1, BAL205-1: van der Ham *et al.* 2009:186 (in tbl.), 189 (tbl. 2), 191 (fig. 5).
Keratoisidinae sp. I4: van der Ham *et al.* 2009: 188 (fig. 3).
BAL2081 Undescribed Keratoisidinae: Pante *et al.* 2012: Fig. 2, fig. 3, suppl table S1
Isidella sp.1 Heestand Saucier *et al.* 2021
"Clade I4" Watling *et al.* 2022

Type series.

Holotype.

Balanus Seamount, New England Seamount chain, Atlantic Ocean; specimen BAL205-1; collected 01 Sept 2005; 39°24.91'N, 65°24.66'W; 1889 m; YPM IZ107121; GenBank acc. # PP838399 (*mtMutS*), PP820651 (*igr4*).

Paratypes.

Balanus Seamount, New England Seamount chain, Atlantic Ocean; specimen BAL208-1; collected 01 Sept 2005; 39°24.88'N, 65°24.65'W; 1815 m; YPM IZ44539; GenBank acc. no. EF622534 (mitochondrion, complete genome), FJ358837 (18S).

Bahama Escarpment, south end Cat Is., The Bahamas; specimen CAT206-1; collected 21 March 2009; 24°08.9839'N, 75°12.0675'W; 1255 m; YPM IZ107122; GenBank acc. # PP820653 (*mtMutS*), PP820650 (*igr4*).

Northwest Providence Channel, SW of Great Abaco Is., The Bahamas; specimen NWP107-1; collected 26 March 2009; 25°51.6663'N, 77°16.4249'W; 1263 m; BPBM 2767; GenBank acc. # PP820656 (*mtMutS*), PP820648 (*igr4*); SRA# SAMN03453088[1].

1 Zapata *et al.* (2015) generated transcriptome data from a mixture of RNA extractions from 3 specimens collected in the Bahamas; these data are available on the NCBI Sequence Read Archive. While these sequencing data are not used in this description, we report it here for future reference.

TABLE 1. Collected specimens showing locality data, museum voucher number, relative size (number of upright branches), and GenBank accession numbers.

Specimen #	Museum voucher #	Location	Latitude	Longitude	Depth (m)	Collection Date	# upright branches	GenBank accession #
BAL2051	YPM IZ 107121	Balanus Seamount, New England Seamounts, Atlantic	39.4152	-65.411	1889	1-Sep-2005	11	PP838399 *mtMutS*; PP820651 *igr4*
BAL2081	YPM IZ 44539	Balanus Seamount, New England Seamounts, Atlantic	39.4147	-65.4108	1815	1-Sep-2005	34	EF622534 mitochondrion, complete genome; FJ358837 *18S*
MOL1011	BPBM D2766	Molokai Canyon, Hawaii, Pacific	21.2131	-156.895	635	26-Aug-2006	2	n/a
MOL6011	BPBM D2764	Molokai Canyon, Hawaii, Pacific	21.316	-157.0214	1652	6-Sep-2006	7[2]	PP820657 *mtMutS*
P56891	BPBM D2765	Seamount on Hawaiian Ridge, Pacific	23.0257	-163.1611	1751	31-Oct-2007	17	PP838400 *mtMutS*; PP820645 *igr4*
CAT1071	YPM IZ 107124	Bahama Escarpment, Cat Is. NW, Atlantic	24.7761	-75.676	1468	19-Mar-2009	3	PP820654 *mtMutS*; PP820647 *igr4*
CAT2061	YPM IZ107122	Bahama Escarpment, Cat Is. South, Atlantic	24.1497	-75.201	1255	21-Mar-2009	12	PP820653 *mtMutS*; PP820650 *igr4*
BOO1031	YPM IZ 107123	Bahama Escarpment “interior”, Conception Is./Booby Cay, Atlantic	23.7851	-75.126	1302	22-Mar-2009	23	PP820655 *mtMutS*; PP820646 *igr4*
NWP1071	BPBM D2767	Northwest Providence Channel, Abaco Is. SW, Atlantic	25.8611	-77.2737	1263	26-Mar-2009	41	PP820656 *mtMutS*; PP820648 *igr4*
NEP2044	BPBM D2902	Northeast Providence Channel, Whale Cay, Atlantic	25.4088	-77.7037	1289	29-Mar-2009	3	PP820652 *mtMutS*; PP820649 *igr4*

[2]Estimate; exact number of branches is hard to determine because the collected specimen is broken into several pieces and the only *in situ* image is from the side.

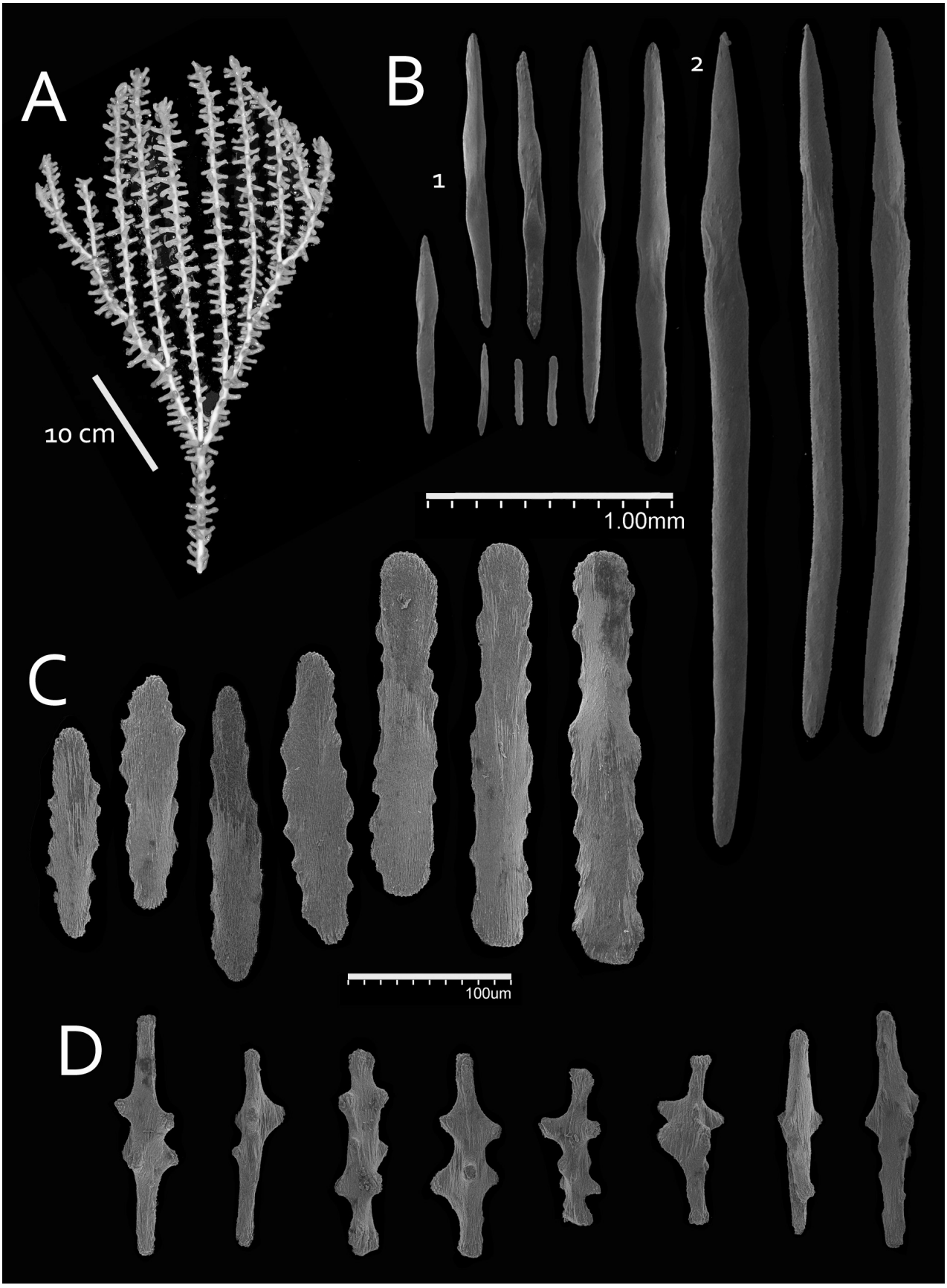

FIGURE 1. *Tridentisis candelabrum*, holotype, BAL205-1, YPM IZ107121, A, collected colony section; and sclerites from, B, the body wall (1, generally, 2, intertentacular sclerites), C, tentacles, and D, the pharynx.

Northeast Providence Channel, Whale Cay, The Bahamas; specimen NEP204-4; collected 29 March 2009; 25°24.5256'N, 77°42.2253'W; 1289 m; BPBM D2902; GenBank acc. # PP820652 (*mtMutS*), PP820649 (*igr4*).

Molokai Canyon, Molokai Island, Hawaii, USA; specimen MOL601-1; collected 06 Sept 2006; 21°18.962'N, 157°01.282'W; 1652 m; BPBM D2764; GenBank acc. # PP820657 (*mtMutS*).

West Twin Bank, Northwestern Hawaiian Ridge, USA; specimen P5-689-1; collected 31 Oct 2007; 23°01.54'N 163°09.669'W; 1751 m; BPBM D2765; GenBank acc. # PP838400 (*mtMutS*), PP820645 (*igr4*).

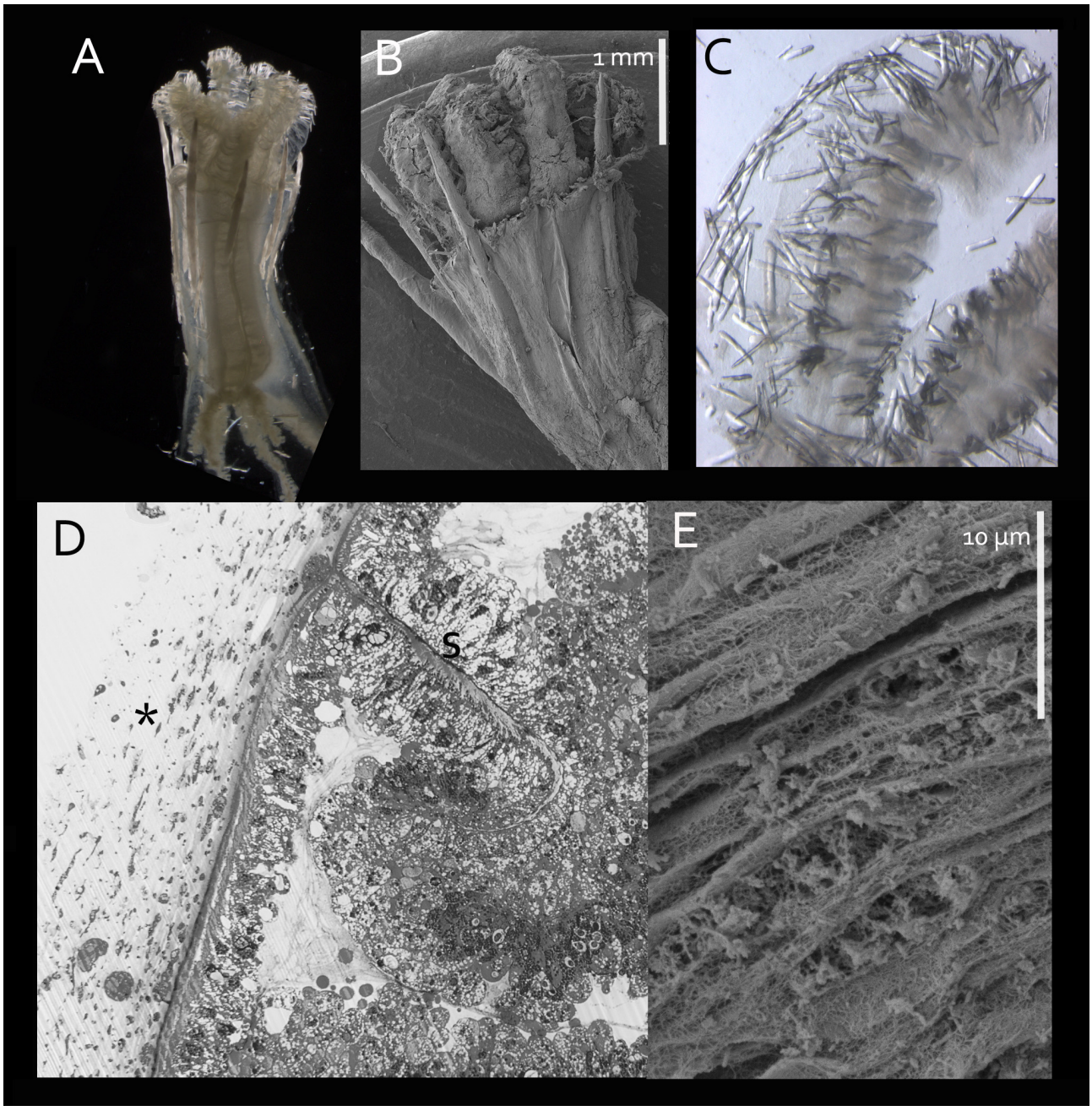

FIGURE 2. *Tridentisis candelabrum*, holotype, BAL205-1, YPM IZ107121, A, whole polyp, tissue cleared with clove oil and imaged with partially crossed polarizing filters. B, scanning electron microscope (SEM) image of upper part of polyp. C, cleared-tissue image of tentacle showing arrangement of sclerites along tentacle rachis and in pinnules. D, light microscope image of thick section cut through the body wall and one septum (s); the outer thick matrix (*) is seen on the left side of the image left of the body wall. E, SEM image of cut through the layered matrix on the outside of the body wall of the polyp; layering appears to be composed of collagen fibers.

Other material examined.

Molokai Island, Hawaii; specimen MOL 101-1; collected 26 August 2006; 21.21313° N, 156.89498° W; 635 m; BPBM D2766.

Bahama Escarpment, Cat Is. NW, The Bahamas; specimen CAT107-1; collected 19 March 2009; 24°46.5670'N, 75°40.5812'W; 1468 m; GenBank acc. # PP820654 (*mtMutS*), PP820647 (*igr4*); SRA# SAMN03453088[1].

S. of Conception Is., The Bahamas; specimen BOO103-1; collected 22 March 2009; 23°47.1077'N, 75°07.6091'W; 1302 m; GenBank acc. # PP820655 (*mtMutS*), PP820646 (*igr4*); SRA# SAMN03453088[1].

Diagnosis. As for the genus.

Description of Holotype. Colony consists of a stalk from which three branches arise from a node in a trident-like fashion (Figure 1A). Each branch subsequently branches at a node four times, producing a candelabra-like colony shape with nine (11, including outermost internodes) vertical branches. Total height of the colony was approximately 70 cm, of which the upper ~40 cm was collected. The central branch is 30 cm long, and the lateral branches range from 27 to 5 cm in length, the shortest being the most lateral. The last internode before the trident is ~7 cm long, the three basal internodes of the trident are 6.0 to 6.7 cm in length, and the internodes leading to the lateral branches are 5.2 to 6.2 cm long. All internodes are approximately 0.4 to 0.5 cm in diameter. The distalmost internodes have large lumens, approximately 50% or more of the diameter, whereas the internodes of the stalk are nearly solid, with very small lumen.

Polyps arise on all sides of the internodes, in sub-opposite or alternating pairs (Figure 1A). Smaller polyps are interspersed among the larger/older polyps suggesting new polyp production occurs continuously. Polyps are more-or-less cylindrical (not tapered), approx. 4 to 9 mm wide/diameter at the base and 5 to 15 mm tall extended when preserved. The pharynx extends 50% or more of the length of the polyp; free edges of mesenteries are thickened at their distal margins where they join the pharynx, giving a "fuzzy" appearance (Figure 2A). Prominent inter-tentacular needles protrude above infolded tentacles and extend basally/proximally to about 50% of the polyp height, but not below pharynx (Figure 2B). Basal half of the polyp (below needles) is mostly free of sclerites (Figure 2A). The exterior of the polyp is covered with a fibrous matrix (Figure 2D,E). When alive, the polyps are transparent (as is the coenenchyme) and with pinkish-red pharynx, giving the appearance of a red mouth and overall pinkish tint to the colony from a distance; the color is lost when preserved in alcohol. *In situ* images show polyps fold the tentacles over the oral disk and do not contract the polyp body to the axis, but rather take on a slightly larger diameter both distally and basally below pharynx to produce a dumbbell-like appearance, e.g. with central constriction.

Sclerites of the polyp comprise prominent needles distally and a scattering of flattened rods proximally (at base of needles) in the body wall, flattened rods on the tentacles, and abundant toothed rods in the pharynx. Needle sclerites are mostly straight and pointed at both ends and range in length from ≈1.0 to 3.4 mm. Flattened rods are bluntly rounded at each end, with or without small tubercles, and range from 0.2 to 0.3 mm in length (Figure 1B). Tentacular sclerites consist of small flattened rods with wavy margins that are bluntly rounded at each end (Figure 1C). They are arranged longitudinally along the "dorsal" side of the tentacle, and extend horizontally into the pinnules (Figure 2C). Tentacle rods range in size from 0.12 to 0.27 mm in length. Pharyngeal sclerites are irregularly toothed rods up to 0.15 mm long. Lateral teeth are relatively large and flat to bluntly rounded (Figure 1D).

The coenenchyme seems to be constructed of the same layered fibrous matrix that is on the polyps and is devoid of sclerites or sclerites are widely scattered and so were not sampled.

Morphological variation.

Numerous examples of this distinct species have been observed and 10 specimens have been collected. The latter range from long stalks with just 3 branches present at the trident junction (Figure 3C,G) to very large colonies with as many as 41 vertical branches (only a few lateral branches were collected; Figure 3E). Some colonies show the narrow branching angle of the holotype (Figure 3A,F), whereas others have much wider angles to the branches (Figure 3B). Usually the density of polyps is such that there is little open space between the branches when the polyps are expanded (Figure 3A,D,I), but in other cases the polyps seem to be quite small (Figure 3B,G).

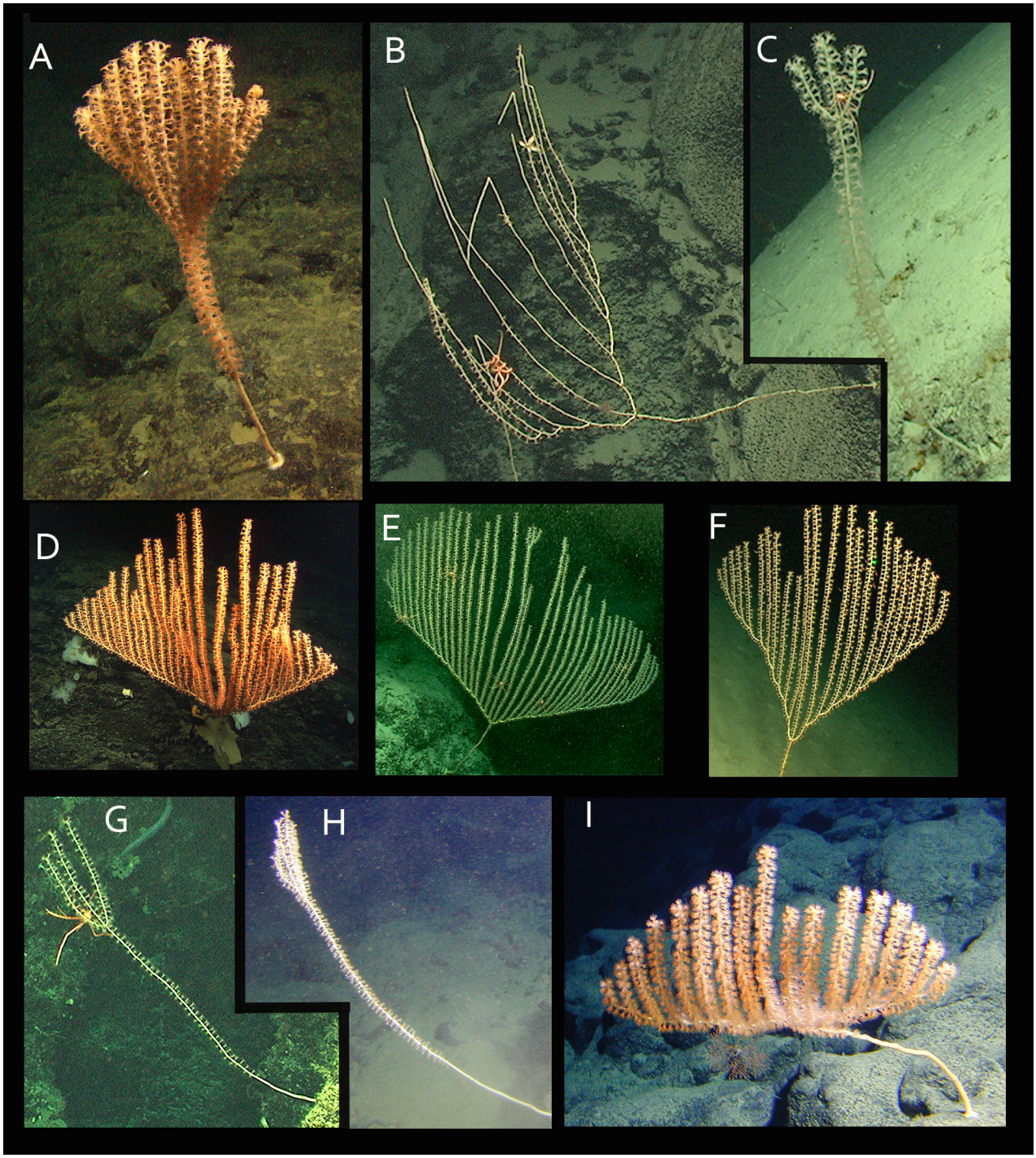

FIGURE 3. Whole colony *in situ* images of *Tridentisis candelabrum* specimens for which samples were collected (see Type Series and Table 1 for details). A, holotype colony (BAL205-1) at 1889 meters depth on Balanus Seamount, New England Seamount chain. B, colony CAT 206-1 from Cat Island, Bahamas, collected at 1255 m. C, paratype colony NEP204-4 at 1289 meters depth in the Northeast Providence Channel, Whale Cay, The Bahamas. D, paratype colony BAL208-1 at 1815 meters depth on Balanus Seamount, New England Seamount chain. E, paratype colony NWP107-1 at 1263 meters depth in the Northwest Providence Channel, SW of Great Abaco Is., The Bahamas; note second-order branching on the central vertical branch creating a second trident. F, colony BOO103-1 at 1302 meters depth south of Conception Is., The Bahamas. G, colony CAT107-1 at 1468 meters depth on the Bahama Escarpment, N. of Cat Is., The Bahamas. H, paratype colony MOL601-1 at 1652 meters depth in Molokai Canyon, Molokai Island, Hawaii. I, paratype colony P5-689-1 at 1751 meters depth on West Twin Bank, Northwestern Hawaiian Ridge.

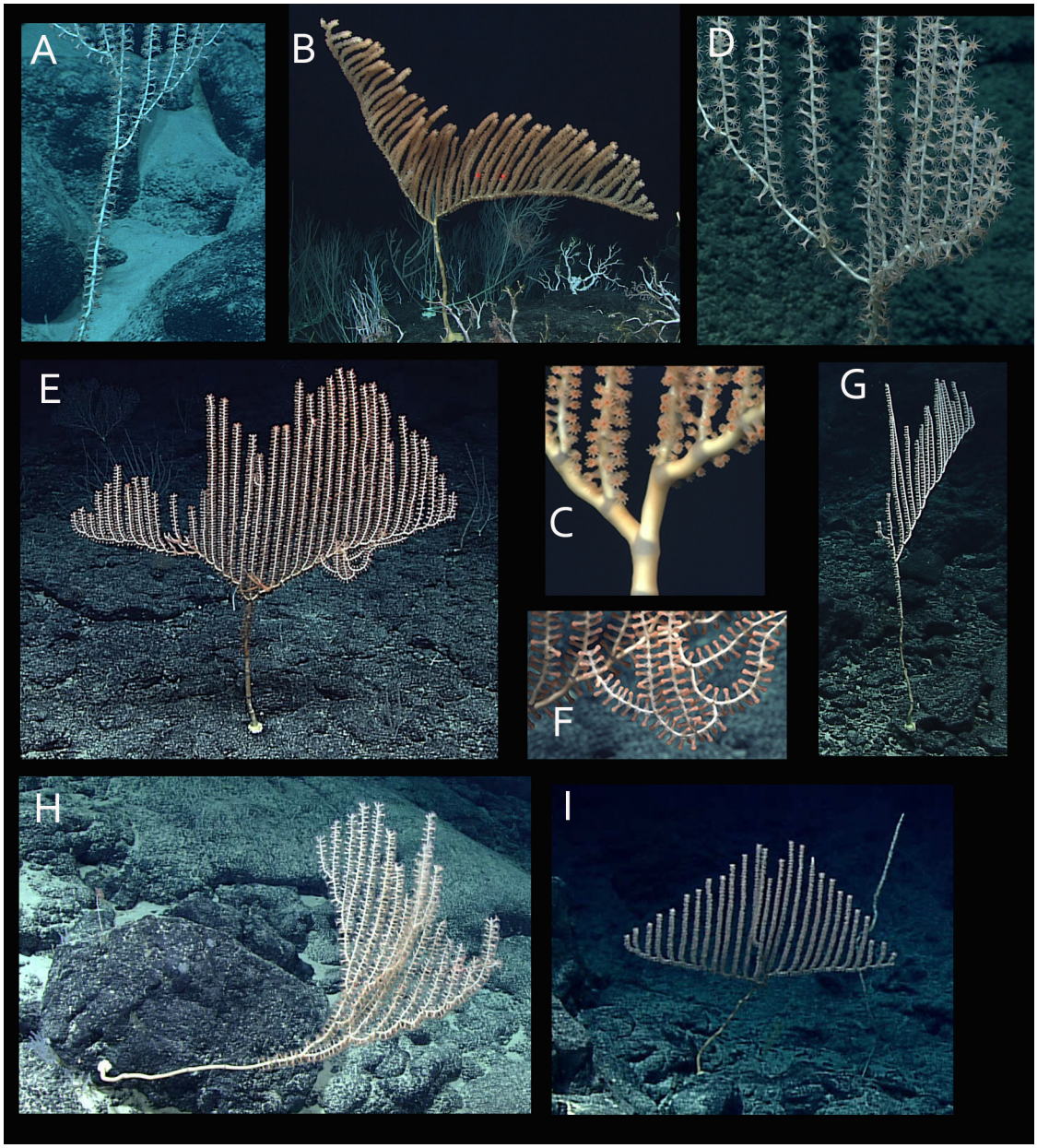

FIGURE 4. Examples of aberrant colony form in *Tridentisis candelabrum*.

A. two-node offset of trident, on rift zone ridge north of St. Rogatien Bank, Northwestern Hawaiian Islands, 1963 m depth, EX1504L2 Dive 3.

B,C. one-node offset of trident, on Mendelsohn Seamount, Musician Seamounts, Pacific Ocean, 1651 m depth, EX1708 Dive 19. A fragment of this colony was collected and sequenced (USNM 1467653; GenBank Acc. # OR805796).

D. asymmetrical branch growth, Explorer Ridge, Mariana Trench Marine National Monument, Pacific Ocean, 1754 m depth, EX1605L3 Dive 15.

E,F. asymmetrical branch growth and anomalous branch "tangle", Karin Ridge, Johnston Atoll Unit of Pacific Remote Islands Marine National Monument, Pacific Ocean, 1897 m depth, EX1504L4 Dive 9.

G. apparent failure of growth of one side of the colony, Wake Atoll Unit of Pacific Remote Islands Marine National Monument, Pacific Ocean, 1972 m depth, EX1606 Dive 7.

H. axis bifurcation one node below trifurcation on one side resulting in branches overlapping and developing out of the plane of the candelabra, Johnston Atoll Unit of Pacific Remote Islands Marine National Monument, Pacific Ocean, 1364 m depth, EX1706 Dive 13.

I. aberrant branching of vertical branch and one node offset of the trident, Wake Atoll Unit of Pacific Remote Islands Marine National Monument, Pacific Ocean, 1982 m depth, EX1606 Dive 3.

Many colonies have been observed by remotely operated vehicles (ROVs), principally during dives in the central Pacific as part of the NOAA CAPSTONE program (Kennedy *et al.* 2019). While a substantial number of those colonies show the normal, nearly symmetrical candelabra form, several aberrant colonies have been observed (Figure 4). Anomalies in the colony growth include asymmetrical branching pattern so that the characteristic trident is not present (Figure 4A,B,C,G,H), unusual branching patterns such as branching from a vertical branch (Figure 4E,H,I), or developing twisting branch tangles (Figure 4E,F), or branches occurring in a plane different from the rest of the candelabra (Figure 4H). A fragment of one aberrant colony from Mendelsohn Seamount in the North Pacific (Figure 4B,C) was collected and sequenced to verify it had a *mtMutS* haplotype to match those of the type series (details below in the Genetics subsection). ROV video observations revealed larger colonies than any that have been collected. For example, sizing lasers trained on a colony from Blake Escarpment showed a width of 1.35 m and height ≈0.8 m (25 cm stem to trifurcation, 55 cm center vertical branch) and 43 vertical branches. The widest colony observed had 61 vertical branches.

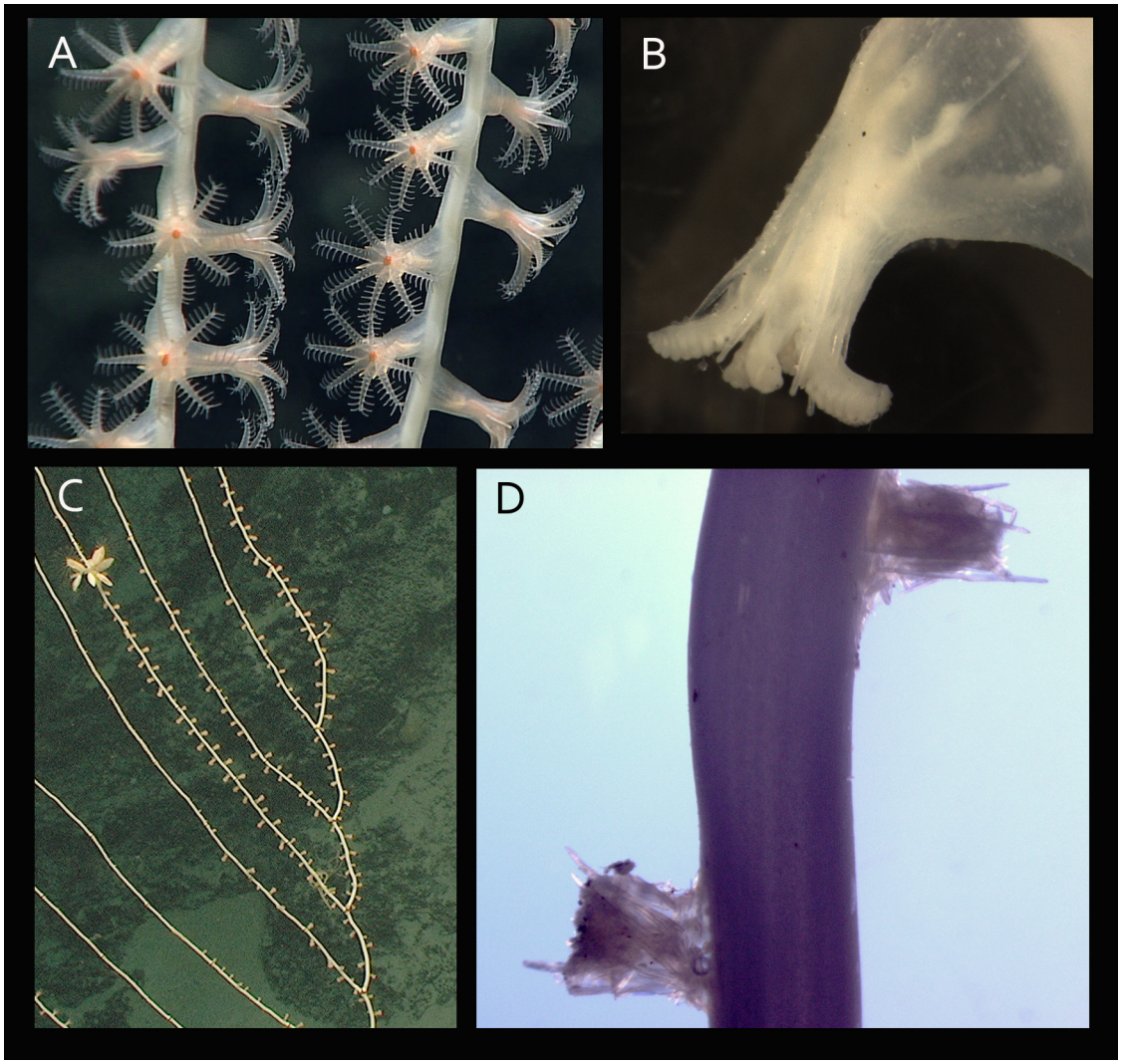

FIGURE 5. Normal and aberrant polyps of *Tridentisis candelabrum* colonies. A. *in situ* image of expanded polyps with projecting inter-tentacular needles, semi-transparent tissue, and red color associated with oral opening (Mariana Trench Marine National Monument, Pacific Ocean, 1847 m depth, EX1605L3 Dive 19). B. microscope image of preserved paratype colony MOL101-1 showing inter-tentacular needles and semi-transparent tissue in the basal part of the polyp. C. *in situ* image of part of the colony CAT 206-1; the widely space branches and sparse polyps are evident. D. microscope image of a section of the most lateral vertical branch; the polyps are poorly developed with only the large needle sclerites being evident.

For the most part, whether the colonies are small, early in their development, or large and mature, full grown polyps have the same morphology. The mature polyp when alive can be translucent in the basal (proximal to the

axis) portion, and light orange to clear in the distal portion, and usually with a red-orange area around the mouth (Figure 5A). With the ROV lighting one can also often see the septally arranged larger needle sclerites extending from the distal part of the body a short distance between the tentacles. The same body translucency and sclerite arrangement can be seen in the polyps of the small[2] colony collected off Molokai, Hawaii (Figure 5B). In contrast, the very sparsely and thin-branched colony collected from deep waters near Cat Island, Bahamas, had very small, poorly developed polyps that appeared to be devoid of the basal, translucent portion (Figure 5C,D). This may reflect differences in growing conditions.

Sclerite preparations were made for the holotype and several paratypes. There is essentially no difference in the sclerome between the holotype and the smallest, and presumed youngest, specimen, MOL 101-1 (Figures 1, 6), with the exception that sclerites were not seen in coenenchyme of the holotype. Unfortunately, sclerites were not examined for the most aberrant specimen, CAT 206-1.

Distribution

Colonies of this new species were collected or observed on seamounts and ridges of the North Atlantic and North and Southwestern Pacific (Figure 7). The depth range of collected samples is 1255 to 1889 m. An additional 112 colonies were identified from video captured during the NOAA CAPSTONE expeditions in 2015–2017 at depths from 1365 to 2214 m, a single colony was observed on Koko Seamount in 2019 at 1910 m during an Emperor Seamounts expedition, four colonies in the Atlantic observed during NOAA ASPIRE expeditions from 2018–2022 in depths from 1263 to 2120 m, and single colonies from deep water off the Great Barrier Reef and another from Annan (Carter) Seamount in the equatorial east Atlantic. The relatively few observations from the Emperor Seamounts and elsewhere, despite many dives and hours on the seafloor within a suitable depth range, suggest this species, though widespread, is generally found in low abundance. On no occasion did we observe multiple colonies growing in close proximity on the seafloor, although the two colonies from Balanus Seamount were 74 m apart.

Genetics

Brugler & France (2008) sequenced the mitogenome of BAL208-1 (paratype YPM IZ44539; GenBank acc. no. EF622534), the first species of Keratoisididae (at the time of publication, a subfamily of Isididae) to have its mitogenome structure determined. The gene order was novel relative to other octocorals and appeared to be a synapomorphy of Keratoisididae, until the recent discovery of the same gene order in a single family of sea pens, Anthoptilidae (Hogan *et al.* 2019, Ganguly and France, 2024). All specimens in the type series share the same haplotypes for mitochondrial gene regions *mtMutS* (approximately 763 bp of the 5' end) and *igr4* (approximately 432 bp), with the exception of MOL601-1, which has poor-quality fragmented sequence resulting in several ambiguous sites. Two specimens (BAL205-1, P5689-1) were additionally sequenced at the *mtMutS* 3'-region (617–848 bp); BAL205-1 showed no differences in this region to the mitogenome of BAL208-1 but P5689-1 showed a single transitional substitution. Interestingly, this same substitution is seen in the aberrant colony from Mendelsohn Seamount (USNM 1467653; GenBank Acc. # OR805796). Both colonies with the sequence variation were from the central North Pacific, while both "BAL" specimens were found on the New England Seamounts in the North Atlantic, suggesting geographic variation that could be further explored in the future. The *Tridentisis* DNA sequences are unique with respect to point substitutions and indel patterns (see below) relative to other Keratoisididae. Van der Ham *et al.* (2009) analyzed different mitochondrial gene regions for their utility as molecular barcodes in Keratoisididae and showed that *Tridentisis* (as "Undescribed A") had a unique indel structure at *igr4*. Pante *et al.* (2012) included BAL208-1 in a molecular phylogeny of the former suborder Calcaxonia (focused on the family Chrysogorgiidae) and Heestand Saucier (2016) showed *Tridentisis* is isolated from other clades of Keratoisididae and later included it as "*Isidella* sp.1" in the revision of the Isididae (Heestand Saucier *et al.* 2021). Watling *et al.* (2022) included BAL208-1 as a representative of "Clade I4" in the phylogeny of Keratoisididae. Morrissey *et al.* (2023) sequenced ultra-conserved elements to get a broad survey of the nuclear genome of Keratoisididae and

2 Under similar growing conditions, we assume the smaller colonies with fewer vertical branches are younger than larger colonies with more vertical branches, but acknowledge that this may not necessarily be the case if increased energy availability in a given location leads to radically higher growth rates.

found the lone representative of *Tridentisis* ("Type I4") included in the phylogeny on a lineage of its own, sister to the J-clade keratoisidids (which includes *Jasonisis thresheri*). We have not had an opportunity to examine this specimen.

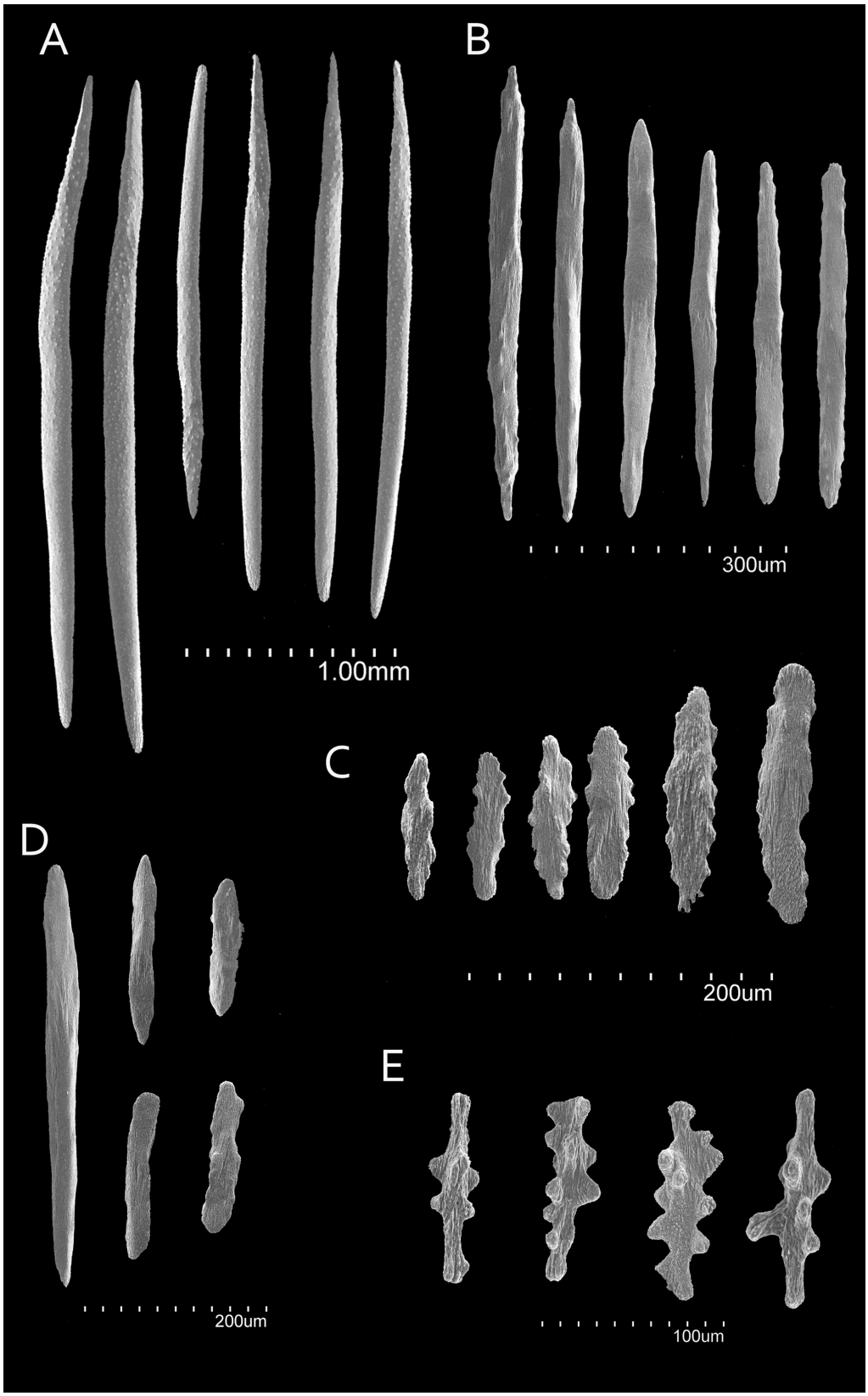

FIGURE 6. *Tridentisis candelabrum*, paratype specimen MOL101-1 sclerites from A, body, intertentacular needles, B, body wall, C, tentacles, D, coenenchyme, and E, pharynx.

France (2007) found frequent insertion/deletion mutations (indels) in alignments of the *mtMutS* gene of Keratoisididae (then Keratoisidinae). Thirteen unique indels, ranging in length from 1 to 16 amino acids, correlated with major clades recovered in the phylogenetic analyses. Bayesian analysis that excluded the indels as characters still recovered the same well-supported clades, indicating that the clades are not simply a reflection of indel structure, *i.e.*, DNA sequence differences independent of indels can distinguish the clades. When Brugler & France (2008) subsequently sequenced the mitogenome of BAL208-1 they discovered it had a *mtMutS* indel structure different from any of the other Keratoisididae. Combined with the unique indel pattern of *igr4* (van der Ham *et al.* 2009) and phylogenetic results of Heestand Saucier (2016), Watling *et al.* (2022), and Morrissey *et al.* (2023), we are confident *Tridentisis* shows both genetic and morphological uniqueness to warrant assignment of genus status.

DISCUSSION

Because octocorals have apical growth and we have never observed a "short-stalked" candelabrum, we hypothesize a colony will have the structure of an unbranched monopod (whip) until the branches that form the initial trident pattern arise, as seen in MOL101-1, which had only one side branch. France (2007) showed that an unbranched monopod/whip is a common growth form independently evolved in several different clades of Keratoisididae (as well as in other octocorals and black corals). However, we have sampled and sequenced many whip-like keratoisidids and we have yet to find one with a genetic signature that suggests it is an early stage *Tridentisis*.

Once colonies of *Tridentisis* have reached a stage where the central trifurcating branches have arisen, it is among the few bamboo corals that is easily recognizable *in situ* from a distance, allowing the use of *in situ* imagery to assess biogeographic distribution. Figure 7 shows that observations of the species are, with a few exceptions, from the northern hemisphere, between 10° and 40°N latitude and 1255 to 2214 m depth, with most observations coming from the North Pacific. However, these observations are biased/limited by the locations of ROV explorations of the NOAA Ship *Okeanos Explorer* from which most of the *in situ* observations came, and we do not yet know the distribution of the species or genus in the Southern Hemisphere (a recent expedition by Schmidt Ocean Institute recorded images of *T. candelabrum* on the Nazca and Sala y Gomez ridges).

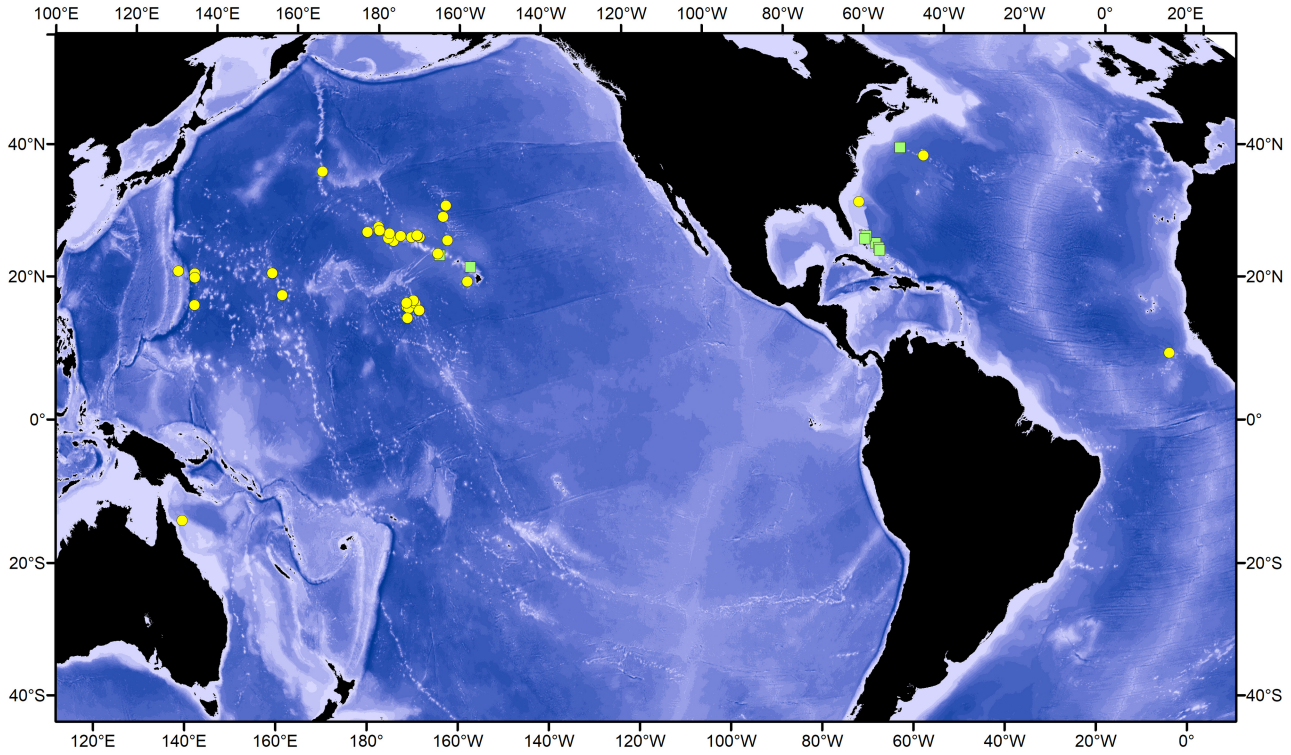

FIGURE 7. Map showing distribution of *Tridentisis candelabrum* specimens, including both collected specimens (green squares) and *in situ* observations from high-definition video from ROV (yellow circles). There is overlap of symbols for collection locations on Balanus Seamount and off Molokai, Hawaii.

The genus *Tridentisis* is unique among the Keratoisididae bamboo corals in having a candelabrum growth form (see Watling *et al.* 2022, Table 4, for comparison with all other clades, some of whom have been described in Lapointe & Watling 2022), although *Isidella tentaculum* Etnoyer, 2008 has a less well-organized candelabrum-like growth pattern (the upright branches frequently give rise to sub-branches, disrupting the "candlestick" appearance). *I. tentaculum* has a sclerome that is predominantly composed of rods whereas *T. candelabrum* has a more diverse sclerome that include needles, rods and flat rods. Also interesting, but not seemingly unique, is the apparent secretion by the epidermis of a thick collagenous layer (Figure 2D,E) that helps to support the polyp in the absence of sclerites, especially in the proximal region of the polyp body.

Relative stages of colonies (younger vs older) can be determined by both number of upright branches and diameter of the central stalk. For any single colony, the trident form is necessarily younger than the candelabrum form since new branches arise from older branches (and not the central stem), and the number of vertical branches increases with age. However, energy availability in a given geographic location will impact growth rates and so absolute age cannot be determined, nor can age comparisons among colonies be made, based solely on these metrics. The largest/widest colony we observed had 61 upright branches. Colonies in the Bahamas appear to have thinner skeletons, although overall colony size can be large in terms of height and number of vertical branches. To our knowledge no attempt has yet been made to age one of these colonies. As keratoisidids grow the skeletal axis can increase in diameter as well as length. It remains unstudied how food availability may affect growth and the "choice" between these two growth processes/directions.

ACKNOWLEDGMENTS

The Atlantic cruises were funded by NOAA Ocean Exploration (formerly Office of Ocean Exploration and Research (OER)): Deep Atlantic Stepping Stones, in 2005, and Deep-water Connections: Probing the Southern Limits of Distribution of North Atlantic Deep-Sea Coral Communities, in 2009, and Schmidt Ocean Institute for the Finding Boundaries in the Sea cruise to the Emperor Seamounts in 2019. Many thanks to Sarah Bingo (Research Corporation of the University of Hawaii) for providing CAPSTONE video annotation data on "clade I4".

We thank our colleagues in the "Deep Atlantic Stepping Stones" and "Deep-water Connections" research groups (J. Adkins, P. Auster, I. Babb, J. Moore, L. Mullineaux, T. Shank and K. Sulak) and the pilots and crews of the ROV *Hercules*, ROV *Global Explorer*, and DSV *Pisces V*, and the R/Vs *F.G. Walton Smith*, *Kaimikai-o-Kanaloa* and NOAA Ship *Ronald H. Brown* for their efforts at sea in helping us secure successful collections, and two anonymous reviewers for comments that improved the manuscript. Watling thanks Robin Beaman and Michelle Taylor for the donation of images and specimens from off the Great Barrier Reef and West Africa, respectively. Also, he wishes to express his greatest appreciation to Tina Carvalho of the University of Hawaii Electron Microscope Facility for her help with thin sectioning and electron microscopy of polyps of the holotype. France thanks M. Brugler, E. Pante, M. Deere, E. Heestand Saucier and J. van der Ham for generating DNA sequence data. Partial support for this work was provided by NOAA's Office of Ocean Exploration (grants nos. NA05OAR4601061 and NA08OAR4600756). This is contribution 222 of the University of Hawaii School of Life Sciences.

REFERENCES

Brugler, M.R. & France, S.C. (2008) The mitochondrial genome of a deep-sea bamboo coral (Cnidaria, Anthozoa, Octocorallia, Isididae): genome structure and putative origins of replication are not conserved among octocorals. *Journal of Molecular Evolution*, 67, 125–136.
https://doi.org/10.1007/s00239-008-9116-2

Etnoyer, P.J. (2008) A new species of *Isidella* bamboo coral (Octocorallia: Alcyonacea: Isididae) from northeast Pacific seamounts. *Proceedings of the Biological Society of Washington*, 121 (4), 541–553.
https://doi.org/10.2988/08-16.1

France, S.C. (2007) Genetic analysis of bamboo corals (Cnidaria: Octocorallia: Isididae): does lack of colony branching distinguish *Lepidisis* from *Keratoisis*?. *Bulletin of Marine Science*, 81 (3), 323–333. [https://www.ingentaconnect.com/contentone/umrsmas/bullmar/2007/00000081/00000003/art00003]

Ganguly, U. & France, S.C. (2024) Expanded distribution and a new genus for rock-inhabiting sea pens (Cnidaria, Anthozoa, Octocorallia, Pennatuloidea). *Zootaxa*, in press.

Heestand Saucier, E. (2016) *Phylogenetic studies of the deep-sea bamboo corals (Octocorallia: Isididae: Keratoisidinae).* PhD dissertation, University of Louisiana, Lafayette, Louisiana, 206 pp.
Heestand Saucier, E., France, S.C. & Watling, L. (2021) Toward a revision of the bamboo corals: Part 3, deconstructing the Family Isididae. *Zootaxa*, 5047 (3), 247–272.
https://doi.org/10.11646/zootaxa.5047.3.2
Hogan, R.I., Hopkins, K., Wheeler, A.J., Allcock, A.L. & Yesson, C. (2019) Novel diversity in mitochondrial genomes of deep-sea Pennatulacea (Cnidaria: Anthozoa: Octocorallia). *Mitochondrial DNA*, Part A, 30 (6), 764–777.
https://doi.org/10.1080/24701394.2019.1634699
Kennedy, B.R., Cantwell, K., Malik, M., Kelley, C., Potter, J., Elliott, K., Lobecker, E., Gray, L.M., Sowers, D., White, M.P. & France, S.C. (2019) The unknown and the unexplored: Insights into the Pacific deep-sea following NOAA CAPSTONE expeditions. *Frontiers in Marine Science*, 6, 480.
https://doi.org/10.3389/fmars.2019.00480
Lapointe, A. & Watling, L. (2022) Towards a revision of the bamboo corals (Octocorallia): Part 5, new genera and species of Keratoisididae from the Tasmanian deep sea. *Zootaxa*, 5168 (2), 137–157.
https://doi.org/10.11646/zootaxa.5168.2.3
McFadden, C.S., Benayahu, Y., Pante, E., Thoma, J.N., Nevarez, P.A. & France, S.C. (2011) Limitations of mitochondrial gene barcoding in Octocorallia. *Molecular ecology resources*, 11 (1), 19–31.
https://doi.org/10.1111/j.1755-0998.2010.02875.x
Morrissey, D., Gordon, J.D., Saso, E., Bilewitch, J., Taylor, M.L., Hayes, V., McFadden, C.S., Quattrini, A.M. & Allcock, A.L. (2023) Bamboozled! Resolving deep evolutionary nodes within the phylogeny of bamboo corals (Octocorallia: Scleralcyonacea: Keratoisididae). *Molecular Phylogenetics and Evolution*, 188, 107910.
https://doi.org/10.1016/j.ympev.2023.107910
NOAA Ocean Exploration (2023) NOAA Ocean Exploration Data Atlas, Version 1.0.4, Available from: https://www.ncei.noaa.gov/maps/ocean-exploration-data-atlas/ (accessed 9 June 2023)
Pante, E., France, S.C., Couloux, A., Cruaud, C., McFadden, C.S., Samadi, S. & Watling, L. (2012) Deep-sea origin and in-situ diversification of chrysogorgiid octocorals. *PLoS One*, 7 (6), e38357.
https://doi.org/10.1371/journal.pone.0038357
Pante, E., France, S.C., Gey, D., Cruaud, C. & Samadi, S. (2015) An inter-ocean comparison of coral endemism on seamounts: the case of *Chrysogorgia*. *Journal of Biogeography*, 42 (10), 1907–1918.
https://doi.org/10.1111/jbi.12564
van der Ham, J.L., Brugler, M.R. & France, S.C. (2009) Exploring the utility of an indel-rich, mitochondrial intergenic region as a molecular barcode for bamboo corals (Octocorallia: Isididae). *Marine Genomics*, 2 (3–4), 183–192.
https://doi.org/10.1016/j.margen.2009.10.002
Watling, L., Heestand Saucier, E. & France, S.C. (2022) Towards a revision of the bamboo corals (Octocorallia): Part 4, delineating the family Keratoisididae. *Zootaxa*, 5093 (3), 337–375.
https://doi.org/10.11646/zootaxa.5093.3.4
Zapata, F., Goetz, F. E., Smith, S.A., Howison, M., Siebert, S., Church, S.H., Sanders, S.M., Ames, C.L., McFadden, C.S., France, S.C., Daly, M., Collins, A.G., Haddock, S.H.D., Dunn, C.W. & Cartwright, P. (2015) Phylogenomic analyses support traditional relationships within Cnidaria. *PLoS ONE*, 10 (10), e0139068.
https://doi.org/10.1371/journal.pone.0139068